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THE MORPHOLOGY OF THE HINGE TEETH OF BIVALVES.

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THE most notable step in advance for the study of bivalve mollusks which has been made for many years is due to the researches of the late F. Bernard, which are included in half a dozen papers, of which the earliest appeared in 1895.

Ever since the time of Schumacher and Lamarck, in the early years of the century, the interlocking projections of the dorsal margins of the valves of pelecypods have been recognized, under the name of hinge teeth, as affording characters of the highest value in systematic classification of the subdivisions of this group. All works treating of these animals have utilized the more or less obvious features of the adult hinge teeth in framing diagnoses of families and genera. Systematists contented themselves, however, with noting the number, position, and division of the teeth into so-called "cardinals" and "laterals" and ignored the fact that large groups have teeth of special types, which can hardly be closely homologized with the teeth characteristic of several other groups. This method of treating the teeth was unquestioned for more than half a century and became so fixed in the minds of systematists that modern efforts to suggest a new point of view have up to the present time been almost futile. Steinmann, in his *Lehrbuch der Paleontologie*, Fischer, in his *Manual* (1887), and especially Neumayr, in his *Morphologie Bivalven Schlosses* (1883), emphasized the necessity of distinguishing between certain fundamental classes or types of hinge teeth, and to Steinmann we owe the suggestion of a formula for indicating in brief form and almost graphic manner the number and relations of the teeth on any given hinge. The writer, in 1889, and Neumayr, in a posthumous paper issued in 1891, applied these principles to the general classification of bivalves, necessarily in a tentative manner, but further advance, or even the confirmation of steps already taken, could be made only on the basis of observed facts of development in concrete cases. Munier-Chalmas (1895) propounded certain theories of prototypic hinges, but in the absence of published observations these attracted slight attention. In the same year the writer elaborated his previous thesis, insisting on the modifications due to dynamic causes acting directly on the hinge, on the origin of hinge teeth from initiative due to external sculpture in the dorsal region, and on the duplex nature of the so-called ligament, which many years before had been recognized by Récluz, whose observations fell on sterile soil. The existence in many nepionic bivalves of a primitive hinge, since named the provinculum, was also pointed out. Almost simultaneously the first of Bernard's papers appeared, for the first time furnishing facts in relation to the development of the hinge teeth in a comparative series of different genera; and thenceforward, until the time of his premature decease, he continued to bring together invaluable data in the same line, covering a large number of genera and opening the way to a field of research of extraordinary promise, throwing an entirely new light on the development of hinge structure and making a permanent breach in the barriers of a conservatism which had so long retarded the appreciation of efforts for a more scientific consideration of the facts of hinge structure. As in all first attempts, the shackles of outgrown methods were not wholly discarded, and much more study is required before a final system can be hoped for, but so much has been done that it is no longer possible for the former inertia to prevail. Several papers bearing on this subject have recently appeared. One of them, by W. von Vest,[1] can be briefly dismissed, as it contributes nothing new in the way of facts and is chiefly devoted to the introduction of a host of new technical German terms, which in turn are reduced to symbols, which when formulated comprise five or six lines of difficultly intelligible letters and figures, requiring three or four times as much more space devoted to "Erklärung der Formel," and, when all is said and done, hinder rather than help. How long will it be before it is universally understood that symbolization which has not the merit of brevity is not only a foolish waste of ingenuity and time but is absolutely without any chance of acceptation?

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[1] Ueber die Bildung und Entwicklung des Bivalven-Schlosses, followed by Entwurf einer Einteilung der lebender Bivalven nach dem Schlossbau, *Verh. des Siebenburgischen Vereins für Naturw. zu Hermannstadt*, Bd. xlviii (1899), pp. 25-150, Pls. I-III.

In this connection it may be noted that Munier-Chalmas proposed a system of notation for the hinge of bivalves which erred not only by involving much purely hypothetical assumption but also by inordinate length. A better was proposed by Bernard, of which some modification is suggested by Dr. Fritz Noetling[1] in an interesting and suggestive paper which has lately reached us. Bernard began work on the teleodont forms (Heterodonta of Neumayr) and under the influence of Munier-Chalmas. As many of the Teleodesmacea have comparable hinges, it was natural that Bernard should suppose that all hinges were comparable and that the formula he proposed should be based on the assumption that from the mere position on the hinge plate the homologies of the individual teeth could be taken for granted, which we believe to be a very mistaken idea. Bernard in his later work realized that error, but unfortunately was not spared to consider the revision of his symbols. As a matter of fact even in the Teleodesmacea Bernard showed before his death that several distinct systems of tooth development can be recognized which cannot be interchangeably homologized. Much more is it impracticable to homologize teeth of such groups as the Prionodesmacea and Teleodesmacea. In groups where it is practicable, — to be determined by observation and not by theory, — Bernard's system will doubtless, with some modification, continue to be used. It is, however, very liable to lead the student unacquainted with its pitfalls into an unprofitable wilderness of theory, when, for the present, facts, and again facts, are imperatively demanded. If we eliminate theory, it still remains important that there should be some symbolical way of presenting the facts to the eye without extended verbal description, and for this we must fall back on some modification of Steinmann's system, which for clearness and brevity can hardly be excelled. It is essential also that the student should not forget that the teeth are not, so to speak, individualities or specific organs, no matter how true they, in the main, are bred from generation to generation. Apart from their genetic origin as the selected results of the dynamic influence of external sculpture on limited areas of the shell (this sculpture itself being a selected consequence of the dynamic influence of the irregularities of the edge of the mantle upon the shell it secretes), the teeth are essentially prominences of a structure of homogeneous material modified by strains and impacts, and an excess or deficiency in the dynamics of the hinge margin in any individual will directly affect the hinge. The proof of this is most obvious in the differences of the lateral lamellæ which will be found in examining a large series from different localities of such a type as Tellina, for instance.

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[1] Notes on the Morphology of the Pelecypoda, *Paleontologia Indica*, N.S., vol. i (1899), pp. 1–43, No. 2. Calcutta.

One important result of Bernard's researches was to show that cardinal and lateral are the disunited segments of an originally continuous lamina, and hence of genetically identical origin in certain teleodonts. In others the cardinals and laterals probably are distinct in origin (Tellina), though these developments so converge that in the adults they would be homologized by any student. The dynamic influence of the ligament when internal is very great and differs at different stages of growth in the same individual. In general it prevents the formation of the "hook," from which cardinal teeth are developed, on the laminæ at the posterior end of the shell, but in some Leptonacea and Crassinella, where the internal resilium is nearly central, prominences which are genetically identical with the so-called cardinals are formed also behind the beaks. The inclination of the teeth to a perpendicular from the beaks is a function of the torsion of the umbonal extremity of the valve and may differ strongly in otherwise closely related species. The cyclodont type of hinge largely results from such torsion. This inclination therefore should not be discussed as if it was an essential character of the teeth in themselves.

For those who may be interested to look into this subject it will be useful to explain the formulæ proposed by Bernard and Steinmann, with their subsequent modifications.

In Bernard's scheme the teeth are numerals, — those of the right valve with odd, and of the left valve with even numerals ; the cardinals have Arabic, the laterals Roman numerals. The character of the teeth is further indicated by capital letters, and their origin by lower case italic letters corresponding to the primitive lamina from which they are supposed to have been detached in the course of development. Bernard begins with the median cardinal and numbers both ways. In most pelecypods the cardinals are all anterior, though the laterals are either anterior or posterior. He begins with the ventral laterals and numbers upwards. One of the interesting points made by Noetling is that the ventral lateral laminæ are sometimes the younger, and therefore the homologies which may be inferred from the numeration beginning below are liable to be disturbed, whereas if the numeration of the laterals began from above, the dorsal laminæ being, as he contends, the older, this source of error would be eliminated.

In our opinion liability to error is inherent in the system which attempts to combine theoretical assumptions as to age and origin with a numerical indication of facts. Laterals may undoubtedly be added above as well as below in the course of growth, for the dorsal margin of the hinge plate is added to as well as the ventral ; the hinge, when the ligament is opisthodetic, or posterior to the beaks of the valves, increases at both edges as long as the shell continues to grow.

Bernard indicates the sockets by a colon and uses the letter L between vertical bars to indicate the place of the ligament. The portion of the ligament which is internal is (so far as known) always the resilium, so it would be better to use R as a symbol, the letter L being already appropriated to symbolize the lateral laminæ. Vertical bars are also used to separate the anterior laterals from the cardinal series, though, as the index letter L or C is already in use as an indicator, the bars do not seem to be needed. If we take as an example the case of a bivalve having three cardinal teeth and two anterior and posterior laterals in each valve, Bernard's formula would be as follows, — the anterior end of the hinge being at the left end of the formula.

Right valve	L A I : III :	Ca 3a : 1 : 3p :	R	L P I : III :
Left valve	L A II : IV	Ca : 2a : 2p : 4p.	R	L P : II : IV

The Steinmann formula for the same shell is:

$$\frac{\mathrm{R\,l\,o\,l\,o\cdot 1\,0\,1\,0\,1\,0\,r\,l\,o\,l\,o}}{\mathrm{L\,o\,l\,o\,l\cdot 0\,1\,0\,1\,0\,1\,r\,o\,l\,o\,l}}.$$

Ordinarily this formula is written in the opposite direction, bringing the left valve above the line, but I have reversed it here to make the formulæ more comparable. In the Steinmann formula we put l for a lateral and 1 for a cardinal; o for a socket, and a period to set off the anterior laterals from the cardinals. In this formula nothing is left to theory: the figures symbolize exactly the number and relative position of the parts of the hinge and a diagram could hardly do it better; of course it is capable of enlargement: for instance, bifid teeth may be symbolized by a fraction ½, instead of a single digit; the amorphous irregularities which occur on such a hinge as that of *Venus mercenaria* may be symbolized by an X, and the soldering of adjacent teeth by the insertion between their symbols of a + sign. All the facts of the hinge of an adult shell can be indicated by this formula. It is only when the facts of the development of any particular hinge have been ascertained that we can use the Bernard formula with equal confidence and accuracy.

The initiation of denticulations on the hinge plate by external sculpture, as pointed out by Neumayr, is illustrated in many of the curious Paleozoic bivalves which he called Paleoconchs. These forms, though not in themselves the oldest known pelecypods, or prototypes, doubtless illustrate the method by which in prototypic forms the organs in question were evolved. Moreover, in the living Mytilidæ, especially the more minute and deep-water forms, the same process in various stages can be directly observed. In some of them, as, for instance, Dacrydium, the development of hinge teeth stops with the completion of the crenulations which in many other pelecypods form only the nepionic hinge or provinculum. The provinculum is common to all the Prionodesmacea, bivalves which include Neumayr's Taxodonta (Arca, Nucula, etc.) and Dysodonta (Mytilus), and other ancient types (Unio, Perna, etc.). A few of the Teleodesmacea (Heterodonta and Desmodonta of Neumayr) also retain traces of it. The marvelous thing in the development of the hinge is that in the vast majority of hinges, including such primitive types as Nucula, the hinge does not go on developing from the provinculum, but the latter stops short and, as it were, after an interval, a wholly new set of teeth, taxodont or other, begins to develop. In the taxodonts there is a multiplication of similar teeth, often more or less /\-shaped, separated by a gap from the most adjacent of the provincular teeth, even when closely similar to them. The explanation of this discontinuity in development is the most interesting question to be solved in connection with the pelecypod hinge. In the Teleodesmacea instead of a multiplication of similar teeth we have a few, usually with one limb, of the /\ disproportionately elongated. The apex of the /\ being adjacent to the umbo, the proximal portions develop into the so-called cardinals on the anterior side of the ligament. Only in forms (Crassinella) having a very symmetrical development is there any indication of a cardinal behind the ligament. The distal end of the long limb of the /\, usually the upper or outer limb, develops into a so-called lateral tooth. This process is characteristic of the forms (Venus, Cyrena, Mactra, etc.) included by Bernard in his cyrenoid type of heterodonts. In others the connection between the processes called cardinals and laterals is practically wanting; the laterals arise separately from the first, as far as observation can determine at present. These are types having the hinge much elongated and the laterals distant (Tellina), or absent (Macoma), or in which the teeth are what I have called cyclodont (Cardium, Isocardia), arising from below the hinge margin and practically without a hinge plate. Most of these were included by Bernard in his lucinoid type of heterodonts. There is nothing to deter us from believing that all these types are fundamentally of common origin ; the few-toothed ledas approach the heterodont type, sometimes very closely; but the divergencies must have begun very early in the history of pelecypods and the differentiation is now very marked. It is earnestly to be hoped that such researches as those of Bernard will be continued until light is thrown on all the various problems for which we now know no suggestion of a solution.

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